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Multivariate and univariate analysis of energy balance data from lactating dairy cows

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ABSTRACT

The objectives of the study were to develop a multivariate framework for analyzing energy balance data from lactating cows and investigate potential changes in maintenance requirements and partial efficiencies of energy utilization by lactating cows over the years. The proposed model accounted for the fact that metabolizable energy intake, milk energy output, and tissue energy balance are random variables that interact mutually. The model was specified through structural equations implemented in a Bayesian framework. The structural equations, along with a model traditionally used to estimate energetic parameters, were fitted to a large database of indirect calorimetry records from lactating cows. Maintenance requirements and partial efficiencies for both models were similar to values reported in the literature. In particular, the estimated parameters (with 95% credible interval in parentheses) for the proposed model were: net energy requirement for maintenance equal to 0.36 (0.34, 0.38) MJ/kg of metabolic body weight·day; the efficiency of utilizing dietary energy for milk production and tissue gain were 0.63 (0.61, 0.64) and 0.70 (0.68, 0.72), respectively; the efficiency of utilizing body stores for milk production was 0.89 (0.87, 0.91). Furthermore, additional analyses were conducted for which energetic parameters were allowed to depend on the decade in which studies were conducted. These models investigated potential changes in maintenance requirements and partial efficiencies over the years. Canonical correlation analysis was used to investigate the association between changes in energetic parameters with additional dietary and animal characteristics available in the database. For both models, net energy requirement for maintenance and the efficiency of utilizing dietary energy for milk production and tissue gain increased in the more recent decades, whereas the efficiency of utilizing body stores for milk production remained unchanged. The increase in maintenance requirements in modern milk production systems is consistent with the literature that describes increased fasting heat production in cows of higher genetic merit. The increase in utilization of dietary energy for milk production and tissue gain was partially attributed to the changes in dietary composition, in particular to the increase in dietary ether extract to levels closer to currently observed in modern milk production systems. Therefore, the estimated energetic parameters from this study can be used to update maintenance requirements and partial efficiencies of energy utilization in North American feeding systems for lactating cows.
Key words: energy, maintenance, efficiency, structural equation

INTRODUCTION

The efficiency with which cows use dietary energy to execute metabolic and production functions has received great attention over the last 5 decades (Moe et al., 1971; Kebreab et al., 2003; Strathe et al., 2011). Estimates of energetic efficiencies and maintenance requirements are necessary for the development of feeding systems and for the examination of production systems through quantitative approaches (Moraes et al., 2012). The North American (NRC, 2001), Dutch (Van Es, 1978), and British (AFRC, 1993) energy evaluation systems for dairy cows rely mainly on data from the 1960s despite dramatic increases in milk production per cow in the past 5 decades (Shook, 2006; VandeHaar and St-Pierre, 2006). Furthermore, cows of high genetic merit have higher gross energetic efficiency than cows of low genetic merit (Veerkamp and Emmans, 1995). Concurrently, genetic selection has increased fasting heat production and energy maintenance requirements in lactating cows (Agnew and Yan, 2000). However, using a European database of indirect calorimetry on

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lactating dairy cows, Strathe et al. (2011) did not find a relationship between maintenance or efficiency parameters and the year studies were conducted. In this context, to cope with increased maintenance requirements and achieve the observed increase in gross energetic efficiency, improvements in energy utilization must have been achieved in at least 1 of the other processes associated with energy transactions in the lactating cow.

Fundamental parameters in energy evaluation systems are partial efficiencies of energy utilization and maintenance requirements. These parameters have been estimated using a variety of modeling approaches for different livestock species. In lactating cows, Moe et al. (1971) proposed a multiple linear regression approach for estimating maintenance requirements and partial efficiencies based on the observation that dietary ME is used with similar efficiencies for maintenance and lactation. Although Kebreab et al. (2003) proposed nonlinear models as alternatives to the multiple regression approach, the nonlinear response functions had similar performance to the multiple regression models. Strathe et al. (2011) proposed an energy function that generalized the model advocated by Moe et al. (1971). These 3 models were univariate, that is, a response variable (usually milk energy output) was regressed on a set of independent variables which were often assumed to be known and measured without error. In this framework, the uncertainty in the observed data is accounted for by the assignment of a probability model for the errors associated with the dependent variable. However, energy balance records have intrinsic variation; for example, measurement error can be expected in intake, fecal, urinary, methane, milk, and tissue energy records. In this context, treating energy traits as independent variables of deterministic nature may underestimate the total variability associated with energetic transactions in the lactating cow, as seminally discussed by Van Es (1972). Furthermore, energy traits are expected to be correlated and mutually interact. For example, biological principles imply that increasing milk production will augment energy intake, and, at the same time, increasing energy intake will increase the delivery of energy available for milk production. Univariate modeling techniques are often unsuitable for the representation of mutually interactive traits. For instance, parameter estimates are biased if 2 mutually interactive traits are used in univariate least squares regression for which 1 trait is used as a covariate to model the other trait (Gianola and Sorensen, 2004). Multivariate models have been proposed for the analysis of energy partitioning in growing animals (Koong, 1977; van Milgen and Noblet, 1999; Strathe et al., 2012). Further, simultaneous and structural equation models have been extensively used in animal breeding (Gianola and Sorensen, 2004; de los Campos et al., 2006; Rosa et al., 2011) and econometrics (Goldberger, 1972; Zellner, 1979; Koop, 2003), but applications in animal nutrition are scarce. Therefore, the objectives of the current study were to propose a multivariate framework for analyzing energy balance data from lactating cows and to investigate potential changes in maintenance requirements and energetic efficiencies associated with changes in dietary characteristics and animals traits over the years.

MATERIALS AND METHODS

Database

The database comprised 1,038 complete energy balance records from 284 Holstein cows in 40 studies conducted from 1963 to 1995. Records summarize at least 4 consecutive days of lactating cows in respiration chambers and were collected at the former USDA Energy Metabolism Unit at Beltsville, Maryland. A comprehensive description of the experimental procedures is available from Flatt et al. (1958) and Moe et al. (1972). The database is a subset of the database described by Moraes et al. (2014), which is composed of measurements on Holstein lactating cows only. Descriptive statistics of nutrient composition of diets and animal status are presented in Table 1. Milk energy output, ME intake, and tissue energy data are presented in Figure 1. The database has a hierarchical structure, such that multiple observations exist on the same animal although animals are not fully nested within studies, as those were used in multiple studies.

General Framework

Models were implemented in a Bayesian framework for which minimally informative prior densities were specified for all parameters and posterior inferences were based on Markov Chain Monte Carlo methods. The Bayesian framework is particularly suited because it naturally accommodates the hierarchical structure of the data and directly estimates standard error of functions of parameters through the Markov Chain Monte Carlo sampling. Models were implemented in the statistical software WinBUGS, which uses Gibbs sampling, Metropolis-Hastings, and slice sampling type algorithms to sample from posterior distributions (Lunn et al., 2000). Two chains with over-dispersed initial values were specified for each parameter, and chain mixing, autocorrelation, posterior densities, and the Gelman-Rubin diagnostics (Gelman and Rubin, 1992) were used to visually assess chain convergence and determine the required burn in period. The tests of the convergence diagnostic and output analysis (CODA)

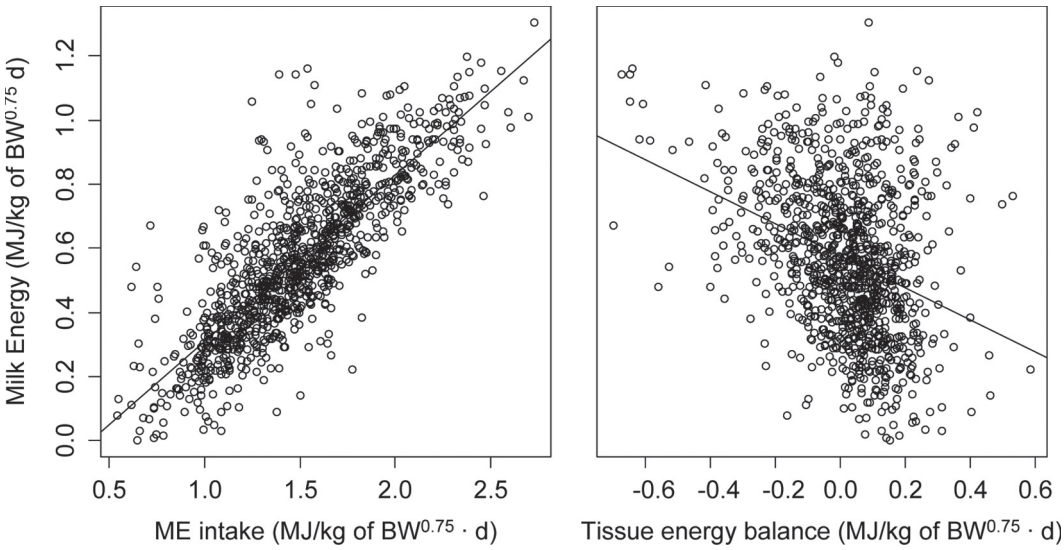

Figure 1. Daily milk energy output (MJ/kg of $BW^{0.75}$·day) versus daily ME intake (MJ/kg of $BW^{0.75}$·day) or daily tissue energy balance (MJ/kg of $BW^{0.75}$·day) with linear trend lines included.

package (Best et al., 1995) were used to formally assess chain convergence. Hypothesis testing of energetic parameters was conducted through the construction of 95% Bayesian credible intervals (**CrI**) and Bayesian *P*-values, defined as *P*-value = 2 × min [$\Pr(\theta_1 - \theta_2 \geq 0|\mathbf{y})$, $\Pr(\theta_1 - \theta_2 < 0|\mathbf{y})$], where Pr = probability, θ_1 and θ_2 are the parameters being compared, and **y** is the observed data. Model comparison was performed using deviance information criteria (**DIC**) as described by Spiegelhalter et al. (2002). The DIC is a model comparison tool that assesses the trade-off between goodness of fit and model complexity and is approximately equal to the Akaike's information criteria in Gaussian models (Ntzoufras, 2009). Specifically, DIC = $\mathrm{E}_{\theta|\mathbf{y}}$ [−2log $p(\mathbf{y}|\boldsymbol{\theta})$] + p_{D}; that is, the expected minus twice the log-likelihood plus a penalty for the number of effective parameters. In this notation, E is the expectation, **y** represents the observed data, **θ** the parameters, and p_{D} is the penalty. In practice, reductions of 5 and 10 DIC units often represent a tendency and a substantive improvement of fit to data, respectively (Spiegelhalter et al. 2002).

Table 1. Descriptive statistics of dietary nutrient composition and animal status[1]

Item[1]	Mean	Minimum	Maximum	SD
NDF (% of DM)	33.7	14.9	76.1	7.2
ADF (% of DM)	19.7	7.7	47.1	4.1
ME (MJ/kg of DM)	10.9	6.9	14.6	0.9
CP (% of DM)	16.3	5.2	23.5	2.5
EE (% of DM)	2.7	1.0	7.0	1.0
DMI (kg/d)	16.8	6.2	29.4	4.2
GEI (MJ/d)	318.5	113.4	584.7	84.1
MEI (MJ/d)	182.1	66.3	348.2	48.1
FECGE (MJ/d)	109.0	23.4	232.6	34.1
UGE (MJ/d)	10.6	2.9	25.6	3.3
CH_4 (MJ/d)	16.8	3.8	30.7	5.0
TEB (MJ/d)	2.6	–86.0	78.8	19.8
MILKGE (MJ/d)	68.6	0.3	156.5	29.3
Milk yield (kg/d)	23.9	0.1	56.6	10.2
Milk CP (%)	3.23	2.30	5.75	0.38
Milk fat (%)	3.58	1.43	7.60	0.71
DIM	160.2	11	488	81.5
BW (kg)	608.1	350.7	854.1	72.4
Age (mo)	64.3	25	185	25.5

[1]EE = ether extract; GEI = gross energy intake; MEI = metabolizable energy intake; FECGE = fecal gross energy output; UGE = urinary gross energy output; TEB = tissue energy balance; MILKGE = milk gross energy output.

Energy Balance Models

Two models were used to describe energy utilization by lactating cows in our study. The first model (Strathe et al., 2011) is a generalization of the model proposed by Moe et al. (1971) and belongs to the family of univariate models because the response represents a single energy trait. The second model belongs to the family of multivariate models for which the response vector is composed of 3 energy traits that were described through structural equations. Herein, q is the metabolizability (MJ of ME/MJ of gross energy), $\mathrm{ME_M}$ is the ME requirement for maintenance (MJ/kg of $\mathrm{BW}^{0.75}$·day), k_L is the efficiency of utilizing dietary ME for milk production (MJ of milk/MJ of ME), k_T is the efficiency of utilizing body stores for milk production (MJ of milk/MJ of tissue), and k_G is the efficiency of utilizing dietary ME for tissue gain (MJ of tissue/MJ of ME).

Univariate Framework. The energy function proposed by Strathe et al. (2011) is described as

$$\mathrm{EL} = \beta_0 + \beta_1\mathrm{MEI} - \beta_2\mathrm{TG} + \beta_3\mathrm{TL}, \qquad [1]$$

where EL denotes the milk energy output (MJ/kg of $\mathrm{BW}^{0.75}$·day), MEI is the dietary ME intake (MJ/kg of $\mathrm{BW}^{0.75}$·day), TG is the tissue gain (MJ/kg of $\mathrm{BW}^{0.75}$·day), and TL is the tissue loss (MJ/kg of $\mathrm{BW}^{0.7}$·day); note that TL and TG are zero if the cow is in positive or negative tissue energy balance, respectively; β_0 is the intercept and β_1, β_2, and β_3 are the parameters describing the change in EL with unit changes in MEI, TG, and TL, respectively. In this model, $\mathrm{NE_M} = -\beta_0$, $\mathrm{ME_M} = -\dfrac{\beta_0}{\beta_1}$, $k_L = \beta_1$, $k_T = \beta_3$, and $k_G = \dfrac{\beta_1}{\beta_2}$, as described in Strathe et al. (2011). The model was implemented through a linear mixed effects model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta} + \boldsymbol{\varepsilon}, \qquad [2]$$

where $\mathbf{y}$ is the $n \times 1$ vector of milk energy outputs; $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are known design matrices relating elements of $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, and $\boldsymbol{\delta}$ to $\mathbf{y}$; $\boldsymbol{\beta}$ is the $m \times 1$ vector of regression coefficients; $\boldsymbol{\alpha}$ is the vector of $mn_a \times 1$ animal random regression coefficients; $\boldsymbol{\delta}$ is the vector of $mn_s \times 1$ study random regression coefficients; and $\boldsymbol{\varepsilon}$ is the $n \times 1$ vector of errors. In this notation, n represents the number of observations, and n_s and n_a are the number of studies and animals, respectively. The joint distribution of the errors and random effects was assumed to be

$$\begin{bmatrix}\boldsymbol{\varepsilon}\\ \boldsymbol{\alpha}\\ \boldsymbol{\delta}\end{bmatrix} \sim N\left\{\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix}, \begin{bmatrix}\sigma^2\mathbf{I}_{\mathbf{n}} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_{\mathbf{n_a}} \otimes \mathbf{G}_\alpha & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}_{\mathbf{n_s}} \otimes \mathbf{G}_\delta\end{bmatrix}\right\}, \qquad [3]$$

where $\otimes$ is the Kronecker product, σ^2 is the errors' variance, $\mathbf{I}$ is the identity matrix, $\mathbf{G}_\alpha$ and $\mathbf{G}_\delta$ are unstructured covariance matrices of order m. In short, the linear mixed effects model represents milk energy output as a linear function of ME intake and tissue energy balance. The effects of these explanatory variables are described by a set of fixed effects representing overall population parameters and also random effects of animal and studies. Random effects represent deviations in the estimated parameters for each animal and study, which are considered to be a sample from a larger population of animals and studies, respectively. The mixed model approach takes into account the correlation of observations originated from the same animal and study. A comprehensive description of the Bayesian implementation of this linear mixed model is provided in Appendix 1.

Multivariate Framework. The multivariate framework proposed in our study differs from traditional univariate models of energy utilization in 2 main aspects: (1) ME intake, milk energy, and tissue energy are all treated as random variables, and (2) ME intake, milk energy, and tissue energy are mutually interactive random variables. The energy functions proposed in this study are

$$\begin{bmatrix}\mathrm{MEI}\\ \mathrm{EL}\\ \mathrm{TE}\end{bmatrix} = \begin{bmatrix}\beta_1\,\mathrm{GEI}\\ \beta_2 + \lambda_{21}\mathrm{MEI} + \lambda_{23}^{(1)}\,\mathrm{TE}\,\mathrm{I}_{\{\mathrm{TE}>0\}} + \lambda_{23}^{(2)}\,\mathrm{TE}\,\mathrm{I}_{\{\mathrm{TE}<0\}}\\ \beta_3 + \lambda_{31}\mathrm{MEI} + \lambda_{32}\mathrm{EL}\end{bmatrix}, \qquad [4]$$

where MEI is the ME intake (MJ/kg of $\mathrm{BW}^{0.75}$·day), EL is the milk energy output (MJ/kg of $\mathrm{BW}^{0.75}$·day), TE the tissue energy balance (MJ/kg of $\mathrm{BW}^{0.75}$·day), GEI is the gross energy intake (MJ/kg of $\mathrm{BW}^{0.75}$·day), and $\mathrm{I}_{\{B\}}$ denotes the indicator function for the event B (i.e., $\mathrm{I}_{\{B\}} = 1$ if B is true and 0 otherwise). In this model, $q = \beta_1$, $\mathrm{NE_M} = -\beta_2$, $\mathrm{ME_M} = -\dfrac{\beta_2}{\lambda_{21}}$, $k_L = \lambda_{21}$, $k_T = -\lambda_{23}^{(2)}$, and $k_G = -\dfrac{\lambda_{21}}{\lambda_{23}^{(1)}}$. The model was implemented through structural equations as described by Gianola and Sorensen (2004):

$$\boldsymbol{\Lambda}\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta} + \boldsymbol{\varepsilon}, \qquad [5]$$

where $\mathbf{y}$ is the $3n \times 1$ vector composed of ME intakes, milk energy outputs, and tissue energy balances; $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are known design matrices relating elements of $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, and $\boldsymbol{\delta}$ to $\mathbf{y}$; $\boldsymbol{\beta}$ is the $m \times 1$ vector of regression coefficients ($m = \sum_{r=1}^{3} m_r$, where m_r is the number of regression parameters for the rth response; the responses are ME intake, milk energy output, and tissue energy balance); $\boldsymbol{\alpha}$ is the $mn_a \times 1$ vector of animal random regression coefficients; $\boldsymbol{\delta}$ is the $mn_s \times 1$ vector of study random regression coefficients; and $\boldsymbol{\varepsilon}$ is the $3n \times 1$ vector of errors. In this notation, n represents the number of observations, n_a the number of animals, and n_s the number of studies. Further, $\boldsymbol{\Lambda} = \mathbf{I_n} \otimes \boldsymbol{\Lambda_0}$, where:

$$\Lambda_{\mathbf{0}} = \begin{bmatrix} 1 & -\lambda_{12} & -\lambda_{13} \\ -\lambda_{21} & 1 & -\lambda_{23} \\ -\lambda_{31} & -\lambda_{32} & 1 \end{bmatrix}, \quad [6]$$

for which the off-diagonal elements are the structural parameters (gradient of 1 energy trait with respect to the other). The unknown elements of $\boldsymbol{\Lambda}$ are collected in $\boldsymbol{\lambda}$, which is modeled as $\boldsymbol{\lambda} = \mathbf{W}\boldsymbol{\lambda}_{\boldsymbol{\mu}} + \mathbf{Z}_3\boldsymbol{\zeta} + \mathbf{Z}_4\boldsymbol{\xi}$, where $\mathbf{W}$, $\mathbf{Z}_3$, and $\mathbf{Z}_4$ are known incidence matrices relating elements of $\boldsymbol{\lambda}_{\boldsymbol{\mu}}$, $\boldsymbol{\zeta}$, and $\boldsymbol{\xi}$ to elements in $\boldsymbol{\lambda}$; $\boldsymbol{\lambda}_{\boldsymbol{\mu}}$ is the $k \times 1$ vector of population structural coefficients (k denotes the number of unknowns in $\boldsymbol{\Lambda_0}$); $\boldsymbol{\zeta}$ and $\boldsymbol{\xi}$ are $kn_a \times 1$ and $kn_s \times 1$ vectors of animal and study random coefficients, respectively. The joint distribution of the errors and random effects was assumed to be:

$$\begin{bmatrix} \boldsymbol{\varepsilon} \\ \boldsymbol{\alpha} \\ \boldsymbol{\delta} \\ \boldsymbol{\zeta} \\ \boldsymbol{\xi} \end{bmatrix} \sim N\left\{ \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{I_n} \otimes \mathbf{R} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I_{n_a}} \otimes \mathbf{G}_{\alpha} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I_{n_s}} \otimes \mathbf{G}_{\delta} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I_{n_a}} \otimes \mathbf{G}_{\zeta} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I_{n_s}} \otimes \mathbf{G}_{\xi} \end{bmatrix} \right\}, \quad [7]$$

where $\mathbf{R}$ is an unstructured covariance matrix of order 3, $\mathbf{G}_{\boldsymbol{\alpha}}$ and $\mathbf{G}_{\boldsymbol{\delta}}$ are unstructured covariance matrices of order m, and $\mathbf{G}_{\boldsymbol{\zeta}}$ and $\mathbf{G}_{\boldsymbol{\xi}}$ are unstructured covariance matrices of order k. We set $\lambda_{12} = 0 = \lambda_{13}$ to create the causal structure described in Figure 2. In this structure, tissue energy balance and milk energy output have a simultaneous relationship in the sense that it may be expected that cows mobilize tissue reserves to sustain milk production, but cows also have increased milk production as a consequence of tissue mobilization. Further, ME intake is assumed to affect milk energy output and tissue energy in a unidirectional fashion because cows often have predetermined intake levels in energy balance calorimetric studies. In short, the multivariate structure of this model allows for the covariance between energy traits to be represented, as well as for the assignment of a probability model comprising the 3 traits. Further, the structural parameters allow the specification of simultaneous and recursive relationships between the response variables. The model also has a mixed model representation describing the relationship between the response vector with fixed and random effects. A comprehensive description of the Bayesian implementation of this structural equation model is presented in Appendix 1.

Changes in Energetic Parameters over the Years

To examine potential changes in energetic parameters over the years, further analyses were conducted in which regression and structural parameters were allowed to depend on the decade the study was conducted. A 3-level nominal factor was created to identify the membership of each record to 1 of the 3 intervals: 1963 to 1973, 1974 to 1983, and 1984 to 1995. Therefore, energetic parameters were decade-specific and the hypothesis that maintenance requirements and energetic efficiencies have changed over the decades was investigated. Canonical correlation analysis (**CCA**) was then used to investigate the correlations between estimated energetic parameters on the different decades and additional dietary characteristics and animal traits

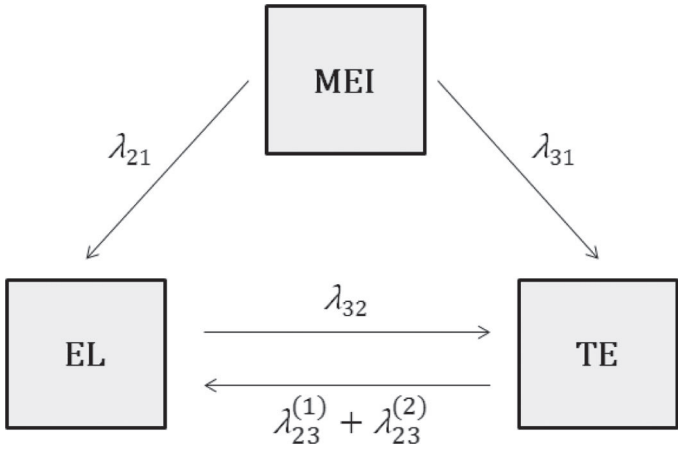

Figure 2. Schematic diagram representing the structural equation model with recursive and simultaneous relationships of energy traits. MEI = metabolizable energy intake (MJ/kg $BW^{0.75}$·day); EL = milk energy output (MJ/kg $BW^{0.75}$·day); TE = tissue energy balance (MJ/kg of $BW^{0.75}$·day). We use the notation from Gianola and Sorensen (2004), where λ are the structural parameters representing the gradients of 1 energy trait with respect to another and not fluxes. In this notation, λ_{23} is the sum of 2 parameters which individually represent the gradient when cows are in positive or negative tissue energy balance. It is important to note that in Equation [4], $\lambda_{23}^{(1)}$ vanishes when the cow is in negative tissue energy balance whereas $\lambda_{23}^{(2)}$ vanishes when the cow is in positive tissue energy balance.

available in the database. The ideal situation would be to identify dietary characteristics and animal traits that affect energetic parameters and model these parameters as a function of such variables within the model-fitting process. The strategy of modeling energetic parameters as a function of dietary characteristics has been adopted by the ARC (1980), where k_L is modeled as a linear function of q. Similarly, Marcondes et al. (2013) modeled partial efficiencies of ME use for maintenance (k_M) and k_G as functions of animal characteristics in beef steers, although a 2-stage type of analysis was adopted. In the present study, an attempt was made to model energetic parameters as a function of dietary variables and animal traits simultaneously in the model fitting, but most of the relationships were not statistically significant. A possible cause for the lack of significant relationships among energetic parameters, dietary characteristics, and animal traits is the mostly unknown forms of the relationships that, in the current study, were assumed to be linear. These results are consistent with Strathe et al. (2011), in which no significant effects of q was found on NE_M, k_L, and k_T when their full data set was used in the analysis. It is important to note, however, that when excluding 2 experiments for which q <0.5, Strathe et al. (2011) found k_L to be significantly affected by q. In this context, CCA was used to describe the association between changes in energetic parameters at different decades with diet and animal characteristics and to potentially elucidate mechanisms associated with the increased gross energetic efficiency of dairy cows in modern production systems through physiology, diet, and milk production.

The CCA was conducted as follows: Let $\boldsymbol{\theta} = (NE_{M,ijl}, k_{L,ijl}, k_{T,ijl}, k_{G,ijl})^T$ be the 4 × 1 vector of mixed effects estimated in the Strathe et al. (2011) model for the lth record ($l = 1, \ldots, n_{ij}$) from the ith animal ($i = 1, \ldots, n_a$) in the jth study ($j = 1, \ldots, n_s$) and $\boldsymbol{\eta} = (HB_{ijl}, DIP_{ijl}, MY_{ijl}, MP_{ijl}, MF_{ijl}, NDF_{ijl}, CP_{ijl}, EE_{ijl}, TEB_{ijl}, DIM_{ijl})^T$ be a 10 × 1 vector of covariates associated with this record describing dietary characteristics and animal traits; here and throughout, superscript T denotes the transpose of a vector or matrix. In this notation, HB is the heart rate in beats per minute, DIP is the days in pregnancy, MY is the milk yield (kg/d), MP is the milk CP (%), MF is the milk fat (%), EE is the dietary ether extract (% of DM), and TEB is the tissue energy balance (MJ/d). It is assumed that

$$\mathrm{Var}\begin{bmatrix}\boldsymbol{\theta}\\ \boldsymbol{\eta}\end{bmatrix} = \begin{bmatrix}\mathbf{V}_{11} & \mathbf{V}_{12}\\ \mathbf{V}_{21} & \mathbf{V}_{22}\end{bmatrix}, \quad [8]$$

where $\mathrm{Var}(\boldsymbol{\theta}) = \mathbf{V}_{11}$, $\mathrm{Var}(\boldsymbol{\eta}) = \mathbf{V}_{22}$, and $\mathbf{V}_{12} = \mathrm{Cov}(\boldsymbol{\theta}, \boldsymbol{\eta}) = \mathbf{V}_{21}^T$ for $\mathbf{V}_{11}$ and $\mathbf{V}_{22}$ of full rank. Canonical correlation analysis identifies vectors $\mathbf{a}$ and $\mathbf{b}$ $\left(\mathbf{a} \in \mathbb{R}^4 \text{ and } \mathbf{b} \in \mathbb{R}^{10}\right)$ such that the correlation between the linear combinations $\mathbf{a}^T\boldsymbol{\theta}$ and $\mathbf{b}^T\boldsymbol{\eta}$ are maximized. In this notation, $\mathbb{R}^n = \left\{(x_1,\ldots,x_n) : x_1,\ldots,x_n \in \mathbb{R}\right\}$. In particular, the function

$$\rho = \max_{\mathbf{a},\mathbf{b}} \left\{ \frac{\mathbf{a}^T\mathbf{V}_{12}\mathbf{b}}{\sqrt{\mathbf{a}^T\mathbf{V}_{11}\mathbf{a}\mathbf{b}^T\mathbf{V}_{22}\mathbf{b}}} \right\}, \quad [9]$$

may be maximized with generalized eigenvalues. The canonical correlations ($\rho_1 \geq \ldots \geq \rho_4$) are the correlations between the canonical variates $\left(\mathbf{a}_1^T\boldsymbol{\theta}, \ldots, \mathbf{a}_4^T\boldsymbol{\theta}\right)$, which are associated with the vector of energetic parameters and the canonical variates $\left(\mathbf{b}_1^T\boldsymbol{\eta}, \ldots, \mathbf{b}_4^T\boldsymbol{\eta}\right)$ associated with the vector of dietary and animal characteristics. Canonical loadings and cross-loadings represent the correlation between each individual variable with its own canonical variate and with the canonical variate of the other set of variables respectively. These measures of correlation are often the ones used to investigate the role of individual variables in the canonical functions because canonical weights are not robust to multicollinearity (Alpert and Peterson, 1972; Hair et al., 1998). In our study, the loadings and cross-loadings of the first canonical functions were used to investigate the correlation between estimated energetic parameters in each decade with dietary and animal characteristics. For example, the canonical loadings of variables in $\boldsymbol{\theta}$ represent the correlation between each individual variable of $\boldsymbol{\theta}$ and the canonical variate $\mathbf{a}_1^T\boldsymbol{\theta}$, whereas canonical cross-loadings of variables in $\boldsymbol{\theta}$ represent the correlation between each individual variable in $\boldsymbol{\theta}$ with the canonical variate $\mathbf{b}_1^T\boldsymbol{\eta}$. The CCA for the structural equation model is similar to the one described previously for the Strathe et al. (2011) model, but with $\boldsymbol{\theta} = (NE_{M,ijl}, k_{L,ijl}, k_{T,ijl}, k_{G,ijl}, q_{ijl})^T$ and $\mathbf{a} \in \mathbb{R}^5$. The CCA was implemented using the yacca package from the statistical software R (Butts, 2012) and a detailed mathematical description of the CCA is presented in Appendix 1.

RESULTS AND DISCUSSION

Energetic Parameters

Posterior means and 95% CrI of all parameters estimated with the univariate Strathe et al. (2011), and the multivariate structural equation models as well as the estimated variance components are presented in Appendix 2 (see Tables A2.1, A2.2, A2.3, and A2.4). Energetic parameters are summarized by posterior means and 95% CrI in Table 2. Diagnostic plots for assessing fit of all models are presented in Appendix

3 (see Figures A3.1 and A3.2). Estimates of the efficiency of utilizing dietary ME for producing milk from both models were similar to the k_L proposed by Moe et al. (1972) and adopted by the NRC (2001). Specifically, the k_L of 0.64 adopted by the NRC (2001) was contained in the 95% CrI from both Strathe et al. (2011) and structural equation models fitted with this database (Table 2). Moreover, the partial efficiencies of utilizing dietary ME for tissue gain from the 2 models are also in good agreement with the values proposed by Moe et al. (1971). For instance, the k_G estimates of 0.70 and 0.75 in our study were within the theoretical maximum efficiencies (0.7, 0.8) of utilizing dietary energy for growth in ruminants calculated by Baldwin et al. (1980). Further, estimates of k_G in this study were substantially smaller than the ones from Kebreab et al. (2003) and Strathe et al. (2011), who estimated k_G ranging from 0.83 to 0.88 in European dairy cows. The results from our study corroborate findings of Moe et al. (1971), that dietary ME is used as efficiently or better for concurrent growth than for lactation. Moreover, the estimated k_T of 0.80 and 0.89 (Table 2) in our study were in good agreement with the efficiencies estimated by Moe et al. (1971). Additionally, these estimates support the results from Moe et al. (1971), that the indirect net efficiency of producing milk from dietary ME through tissue mobilization and subsequent deposition was similar to k_L. For example, in the structural equation model, this efficiency would be $0.89 \times 0.70 = 0.62$, which is similar to the estimated k_L of 0.63 from this model. Finally, it is important to note that in all models from our study $k_T > k_G$, as originally proposed by Moe et al. (1971) but challenged by Kebreab et al. (2003) and Strathe et al. (2011). In particular, the implementation of the Strathe et al. (2011) model with our database and the estimation of efficiencies, for which $k_T > k_G$, suggests that there may be substantial differences between the European (Kebreab et al., 2003; Strathe et al., 2011) and North American databases rather than differences in the models used to estimate energetic efficiencies. It can therefore be suggested that, in US Holstein cows, the efficiency of producing milk from body store reserves is substantially higher than the efficiency of utilizing dietary ME for tissue energy gain, as initially proposed by Moe et al. (1971). Strathe et al. (2011) pointed out that the majority of records from the European database originated from multiparous cows with a median parity of 3. The authors suggested that body growth was limited and hypothesized that the higher k_G, in comparison with values from Moe et al. (1971), was a consequence of the gain being mostly replenishment of body lipids mobilized at early lactation. Furthermore, body lipid deposition is related to body protein deposition and to the degree of animal maturity, which may be altered by genetic selection (Coffey et al., 2002, 2003). Therefore, differences in k_G from the 2 databases may be a result of the gain compositions and different degrees of cattle maturity at the start of lactation. Furthermore, k_G is theoretically affected by the diet composition (as discussed in the next section) and differences in the nutrient fractions comprising dietary ME have the potential to alter the efficiency of dietary energy utilization. Therefore, changes in the selection of feeds for diet formulation in the 2 databases may also explain differences in k_G. Likewise, k_T represents the efficiency of utilizing body stores to synthesize milk, which was estimated to be substantially larger in this database than estimates from the European database (Kebreab et al., 2003; Strathe et al., 2011). The estimates from our study suggest a high efficiency of utilization of body stores for milk production, which is in good agreement with the NRC (2001). Two main points may explain the differences in estimated tissue related efficiencies in the 2 databases. First, Moe et al. (1971) pointed out that tissue energy balance calculations are subjective to cumulative errors from measurements of ME intake, heat production, and milk energy output, and are therefore the energy fraction associated with the largest error. Second, Strathe et al. (2011) and Moe (1981) discussed the instability in estimating energetic parameters from indirect calorimetry and pointed out the inherent correlation between energetic efficiencies within a model.

Energy maintenance requirements estimated in the 2 models are given in Table 2. The NE_M from the Strathe et al. (2011) model (0.35 MJ/kg of $BW^{0.75}$·day) was in good agreement with the NE_M adopted by the current US feeding system for dairy cows of 0.33 MJ/kg of $BW^{0.75}$·day [or 0.08 Mcal/kg of $BW^{0.75}$·day]. However, the NE_M from the structural equation model (0.36 MJ/kg of $BW^{0.75}$·day) was slightly larger compared with

Table 2. Energetic parameters posterior means and 95% credible intervals (in parentheses) using the Strathe et al. (2011) and the structural equation (SEqM) models[1]

Parameter	Strathe et al. (2011)	SEqM
q	—	0.57 (0.56, 0.58)
ME_M	0.57 (0.53, 0.60)	0.57 (0.54, 0.59)
NE_M	0.35 (0.32, 0.38)	0.36 (0.34, 0.38)
k_L	0.62 (0.60, 0.64)	0.63 (0.61, 0.64)
k_T	0.80 (0.76, 0.84)	0.89 (0.87, 0.91)
k_G	0.75 (0.70, 0.79)	0.70 (0.68, 0.72)

[1] q = metabolizability (MJ of ME/MJ of gross energy); ME_M = metabolizable energy requirements for maintenance (MJ/kg of $BW^{0.75}$·day); k_L = efficiency of utilizing ME intake for milk production (MJ of milk/MJ of ME); k_T = efficiency of utilizing body stores for milk production (MJ of milk/MJ of tissue); k_G = efficiency of utilizing ME intake for tissue gain (MJ of tissue/MJ of ME).

NRC (2001) because the value of 0.33 was outside its 95% CrI (Table 2). The ME_M from models in our study was 0.57 MJ/kg of $BW^{0.75}$·day (Table 2), which is greater than NRC (2001) recommendations that can be calculated based on the default values for NE_M and k_L [$ME_M = NE_M/k_L = 0.33/0.64 = 0.52$ MJ/kg of $BW^{0.75}$·day using $k_M = k_L$, as suggested by the NRC (2001)]. However, the ME_M was within the range of estimates by Agnew and Yan (2000; 0.49 to 0.67 MJ/kg of $BW^{0.75}$·day). A potential increase in maintenance requirements for lactating dairy cows in modern milk production systems was discussed in detail by Agnew and Yan (2000). In particular, the process of genetic selection for milk production may have altered animals' metabolic rates and, consequently, maintenance requirements. For instance, Yan et al. (1997) estimated fasting heat production of Holstein-Friesian cows of 0.45 MJ/kg of $BW^{0.75}$·day, and Birnie (1999) reported fasting heat production of 0.39 MJ/kg of $BW^{0.75}$·day for nonlactating, nonpregnant dairy cows previously fed at maintenance level. Values from both studies were substantially greater than the current NRC (2001) estimate of NE_M (0.33 MJ/kg of $BW^{0.75}$·day). Similarly, 5 decades ago, high-producing lactating cows had a proportional 0.20 increase in ME required for maintenance compared with cows with moderate milk production levels (Flatt et al., 1969; Moe et al., 1970; Van Es et al., 1970). Likewise, beef steers with different residual feed intakes were estimated to have considerably different energy requirements for maintenance (Sainz et al., 2013). A difference of 30% in maintenance requirements was observed between steers in the most- and least-efficient groups. Two major factors were discussed by Agnew and Yan (2000) for explaining changes in maintenance of dairy cows with genetic selection: larger proportions of BW as protein mass and enlarged organ sizes in high-producing lactating cows due to greater nutrient intakes. The fact that modern dairy cows have larger proportions of body protein mass was confirmed by Ferris et al. (1999), who reported that high-genetic merit cows had lower backfat thickness, at comparable BW, than cows of medium and low genetic merits. Similarly, Veerkamp et al. (1994) estimated a higher lipid-free empty BW proportion in high-genetic merit cows. The influence of BW protein proportion in maintenance requirements may be explained by the substantial energy cost associated with protein turnover (Baldwin et al., 1980; Agnew and Yan, 2000). Furthermore, cows of high genetic merit may have enlarged organ sizes due to increased nutrient intakes and a greater activity of digestive and circulatory tissues to digest and transport nutrients, as discussed by Agnew and Yan (2000). Organs involved in these metabolic activities have an important contribution to total maintenance requirements (Baldwin et al., 1980, 1985).

Changes in Energetic Parameters over the Years

The effect of the study decade was introduced into energetic parameters through a 3-level nominal factor. We hypothesized that changes in q, maintenance, and efficiency parameters in the past few decades may elucidate potential mechanisms associated with the increased gross energetic efficiency of dairy cows in modern production systems. The estimated mixed effects (i.e., fixed population parameters plus animal and study deviations from the population) from the different decades were associated with additional variables describing dietary characteristics and animal traits through canonical correlation analysis. We quote Pearson (1900), "... where we find correlation we cannot always predict causation," to point out that the results must be interpreted from a correlation perspective because correlation is a necessary but not sufficient condition for causality. Studies from this database were conducted under distinct biological hypotheses examining various nutritional factors associated with energy utilization in dairy cows. However, the division of this database into decades aimed at representing the changes in animals and diets that would have occurred with the advancement of bioenergetics research and the genetic selection process of animals and feedstuffs over the years.

Posterior means and 95% CrI of the parameters estimated in all models of different decades are presented in Appendix 2. Estimated energetic parameters and associated 95% CrI are presented in Table 3. Metabolizability in the structural equation model was not different between decades, suggesting that diet q did not change across decades in this database. In particular, q was not different between the first and second decade ($P = 0.81$) and the first and third decade ($P = 0.41$). Similarly, k_T was not statistically different among decades for any energy function, suggesting that the efficiency with which cows mobilize body stores to produce milk has not changed over the decades in this database. However, ME_M, NE_M, k_L, and k_G all increased over the decades for both energy functions (Table 3), suggesting that maintenance requirements and the efficiency of utilizing dietary ME increased over the decades in this database. The increased maintenance requirement in high-producing dairy cows has been discussed herein and by Agnew and Yan (2000) comprehensively. In particular, Agnew and Yan (2000) pointed out that high-producing cows have enlarged organ sizes to sustain nutrient transport, digestion, and absorption at rela-

tively greater nutrient intakes. Boxplots of dietary and animal characteristics from the 3 decades are presented in Figure 3. For instance, it is evident that heart rate, milk yield, and gross energetic efficiency are largest in cows of the third decade (Figure 3). Furthermore, the efficiency of utilizing dietary ME for milk production in the first and second decades were not different in the univariate model ($P = 0.18$) as well as in the structural equation model ($P = 0.06$), although the estimated k_L in the second decade is slightly outside the 95% CrI of the k_L from the first decade. Conversely, k_L in the third decade was greater in both univariate ($P < 0.01$) and structural equations ($P < 0.01$) models compared with the first decade. Similarly, k_G was greater in the second decade than in the first in both univariate ($P = 0.01$) and structural equation models ($P = 0.04$). Moreover, k_G was also greater in the third decade than in the first in both univariate ($P < 0.01$) and structural equation ($P < 0.01$) models. Additionally, it is important to notice that models fitted with energetic parameters depending on the study decade were better supported by the data than models fitted without the study decade. A reduction in the DIC was observed for all energy functions when maintenance requirements and energetic efficiencies were decade specific. Specifically, with the Strathe et al. (2011) model, the DIC decreased 6 points and with the structural equation model the DIC decreased 46 points when the parameters were allowed to depend on the study decade.

Canonical correlation analysis was used to investigate the degree of association between the set of estimated energetic parameters at different decades and a set of variables describing dietary and animal characteristics. Particularly, loadings and cross-loadings from the CCA were used to identify animal and dietary characteristics that have high correlations with the canonical variate associated with the estimated energetic parameters in different decades. The number of canonical correlations extracted is equal to the number of variables in the smaller set. The canonical correlations were ($r_1 = 0.83$, $r_2 = 0.41$, $r_3 = 0.40$, $r_4 = 0.20$) for the parameters from the Strathe et al. (2011) model, and ($r_1 = 0.83$, $r_2 = 0.48$, $r_3 = 0.40$, $r_4 = 0.32$, $r_5 = 0.13$) for the parameters from the structural equation model. The first canonical correlations between the 2 sets of variables in both models suggest that, as expected, the canonical variates from the set of dietary animal characteristics and the set of energetic parameters from the different decades were strongly correlated. The canonical weights, loadings, and cross-loadings associated with the first canonical functions are presented in Table 4. In both models, canonical loadings of the energetic parameters were high for the NE_M, k_L, and k_G, suggesting that these 3 energetic parameters were the most important predictors for the first canonical variate associated with the $\boldsymbol{\theta}$ vector. Moreover, the canonical loadings of the dietary and animal variables were high for heart rate, milk yield, and dietary ether extract, suggesting that these 3 variables were the most important animal and dietary contributors for the first canonical function. Similarly, the examination of the cross-loadings of the first canonical function suggests that milk yield, heart rate, and dietary ether extract were the variables that present greater correlations with the canonical variate associated with the set of energetic parameters. Likewise, energetic parameters that correlated highly with the first canonical variate of the set of dietary and animal related variables were NE_M, k_L, and k_G. Furthermore, the redundancy coefficient describes the amount of variance in the energetic parameters' canonical variate explained by the animal- and diet-related canonical variate. These coefficients were 0.49 and 0.38 for the first canonical function for the Strathe et al. (2011) and structural equation models, respectively.

Therefore, using the findings that maintenance requirements and dietary partial efficiencies were different between decades and the results from the CCA, combined dietary and animal factors can be used to explain the increase in the efficiency of utilizing dietary energy. Partial efficiencies of ME utilization for milk production and growth are dependent on stoichiometric and thermodynamic relationships between substrates

Table 3. Energetic parameters posterior means and 95% credible intervals (in parentheses) using the Strathe et al. (2011) and the structural equation (SEqM) models for the 3 decades for which studies were conducted

Parameter[1]	Decade	Strathe et al. (2011)	SEqM
q	1963–1973	—	0.56 (0.55, 0.58)
q	1974–1983	—	0.57 (0.55, 0.59)
q	1984–1995	—	0.57 (0.55, 0.59)
ME_M	1963–1973	0.50 (0.47, 0.54)	0.51 (0.48, 0.54)
ME_M	1974–1983	0.58 (0.53, 0.63)	0.59 (0.55, 0.63)
ME_M	1984–1995	0.70 (0.64, 0.75)	0.74 (0.70, 0.78)
NE_M	1963–1973	0.30 (0.27, 0.33)	0.31 (0.28, 0.33)
NE_M	1974–1983	0.36 (0.32, 0.41)	0.37 (0.34, 0.41)
NE_M	1984–1995	0.48 (0.42, 0.53)	0.52 (0.47, 0.56)
k_L	1963–1973	0.60 (0.58, 0.62)	0.60 (0.58, 0.62)
k_L	1974–1983	0.62 (0.59, 0.65)	0.63 (0.60, 0.65)
k_L	1984–1995	0.68 (0.65, 0.71)	0.70 (0.68, 0.73)
k_T	1963–1973	0.82 (0.76, 0.87)	0.90 (0.89, 0.92)
k_T	1974–1983	0.81 (0.73, 0.87)	0.90 (0.88, 0.93)
k_T	1984–1995	0.79 (0.70, 0.86)	0.90 (0.88, 0.92)
k_G	1963–1973	0.68 (0.63, 0.73)	0.66 (0.64, 0.69)
k_G	1974–1983	0.79 (0.72, 0.87)	0.70 (0.67, 0.73)
k_G	1984–1995	0.83 (0.77, 0.91)	0.78 (0.75, 0.80)

[1] q = metabolizability (MJ of ME/MJ of GE); ME_M = metabolizable energy requirements for maintenance (MJ/kg of $BW^{0.75}$·day); k_L = efficiency of utilizing ME intake for milk production (MJ of milk/MJ of ME); k_T = efficiency of utilizing body stores for milk production (MJ of milk/MJ of tissue); k_G = efficiency of utilizing ME intake for tissue gain (MJ of tissue/MJ of ME).

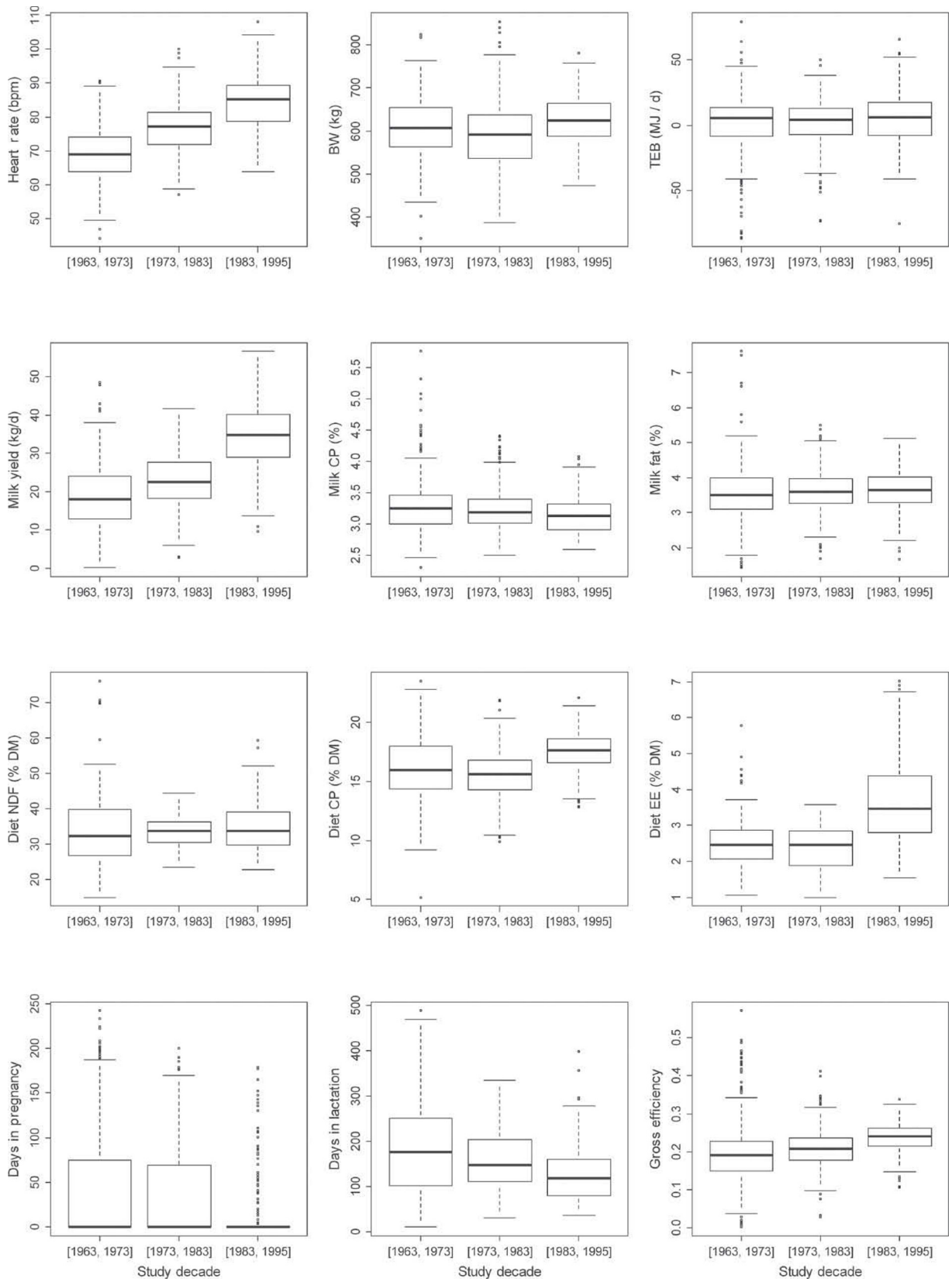

Figure 3. Boxplots of dietary characteristics and animal traits for the 3 decades. TEB = tissue energy balance (MJ/d); EE = ether extract (% of DM); gross efficiency is equal to the ratio of the milk energy output and the gross energy intake.

Table 4. Canonical weights, loadings, and cross-loadings for the first canonical variates of the dietary and animal characteristics and estimated energetic parameters in Strathe et al. (2011) and structural equation (SEqM) models[1]

	Strathe et al. (2011)			SEqM		
Variable[2]	Weights	Loading	Cross-loading	Weights	Loading	Cross-loading
η						
HB	−0.0312	−0.7878	−0.6571	−0.0296	−0.7703	−0.6358
DIP	−0.0002	0.2736	0.2282	0.0005	0.2816	0.2324
MY	−0.0001	−0.8695	−0.7252	−0.0001	−0.8627	−0.7121
MP	−0.2532	0.2618	0.2184	−0.2099	0.2482	0.2049
MF	0.0216	0.0355	0.0296	0.0173	0.0417	0.0344
NDF	−0.0112	0.0302	0.0252	−0.0099	0.0577	0.0476
CP	−0.0465	−0.5216	−0.4350	−0.0694	−0.5574	−0.4601
EE	−0.2635	−0.6877	−0.5736	−0.2174	−0.6569	−0.5422
TEB	−0.0191	−0.0303	−0.0253	−0.0191	−0.0485	−0.0400
DIM	−0.0023	0.4194	0.3498	−0.0038	0.3693	0.3048
θ						
NE_M	−5.1565	−0.9568	−0.7981	−8.5666	−0.9665	−0.7978
k_G	−2.0030	−0.9233	−0.7701	−1077.7401	−0.9308	−0.7683
k_L	−15.0817	−0.9541	−0.7957	1189.1346	−0.9318	−0.7691
k_T	−14.0847	0.3516	0.2933	−974.4818	0.0643	0.0531
q	—	—	—	−2.9921	−0.3225	−0.2662

[1]Weights are the vectors **a** and **b** used to construct the canonical variates $\mathbf{a}^T\boldsymbol{\theta}$ and $\mathbf{b}^T\boldsymbol{\eta}$. Canonical loadings and cross-loadings represent the correlation between each individual variable with its own canonical variate and with the canonical variate of the other set of variables, respectively. The loadings and cross-loadings of the first canonical functions are used to investigate the correlation between estimated energetic parameters in each decade with dietary and animal characteristics. For example, the canonical loadings of variables in **θ** represent the correlation between each individual variable from **θ** and the first canonical variate of **θ**, whereas canonical cross-loadings of variables in **θ** represent the correlation between each individual variable in **θ** with the first canonical variate of **η**.

[2]**η** = vector of dietary and animal characteristics; **θ** = vector of estimated energetic parameters in each decade. HB = heart rate in beats per minute; DIP = days in pregnancy; MY = milk yield (kg/d); MP = milk crude protein (%); MF = milk fat (%); EE = dietary ether extract (% of DM); TEB = tissue energy balance (MJ/d). Further, q = metabolizability (MJ of ME/MJ of GE); k_L = efficiency of utilizing dietary ME for milk production (MJ of milk/MJ of ME); k_T = efficiency of utilizing body stores for milk production (MJ of milk/MJ of tissue); k_G = efficiency of utilizing dietary ME for tissue gain (MJ of tissue/MJ of ME).

and animal products (Baldwin, 1995). For instance, dietary ME utilization is affected by type of diet (Garrett and Johnson, 1983) because changes in dietary composition will alter the pattern of available nutrients for milk and tissue synthesis. Equally, changes in the partial efficiencies of producing milk and depositing tissue energy may occur through changes in milk and tissue gain compositions. Indeed, cows' energy balance status may also alter the energetic efficiency of synthesizing milk: cows mobilizing body fat will use more preformed lipids and less VFA to produce milk fat than cows in positive energy balance. From this database, it can be suggested that cows in the last decade were of higher genetic merit than cows in the first 2 decades, although pedigree information was not available. However, some studies have reported that partial efficiencies of ME utilization are similar for cows of different genetic merits (Grainger et al., 1985; Veerkamp and Emmans, 1995) and also for cows in studies conducted in different decades (Strathe et al., 2011). In addition, Bauman et al. (1985) suggested that between-animal variability in the partial efficiency of utilizing dietary ME for lactation is negligible and proposed alternative strategies for gains in efficiency, such as altered nutrient partitioning and dilution of maintenance. Although cows of different genetic merits have been reported to have similar k_L, there is increasing evidence that genetic selection has altered the expression of genes associated with nutrient utilization pathways. For instance, Holstein-Friesian cows of different genetic backgrounds have been found to have different expression of gluconeogenic enzymes (White et al., 2012). Moreover, changes in subcutaneous adipose tissue metabolism and gene network expression have been reported in cows of different genetic merits (Khan et al., 2013), and the expression of genes involved in the somatotropic axis have been found to differ in different strains of Holstein-Friesian cows (McCarthy et al., 2009). A key factor determining the efficiency of dietary energy utilization is the source of dietary energy (Smith, 1988; VandeHaar, 1998). Diets in the third decade had higher proportion of ether extract than diets in the first 2 decades (Figure 3). It

can therefore be hypothesized that a greater proportion of the dietary ME content originated from fat in the third decade. Such differences in the nutrients comprising dietary ME would alter the nutrients available for production functions and, consequently, alter the efficiencies of producing milk and depositing tissue energy. It is important to note that the dietary ether extract percentages from the first 2 decades (means = 2.47 and 2.37% of DM) were in good agreement with the data (Moe et al., 1971; Moe et al., 1972) used as the basis for the energy evaluation system for the current US feeding system for dairy cows (NRC, 2001). However, the dietary ether extract percentages in the third decade (mean = 3.71% of DM) were closer to dietary ether extract percentages from modern milk production systems (Rossow and Aly, 2013). The increase in k_L with increased dietary fat is well established in the literature and has been traditionally attributed to a decrease in the heat increment (VandeHaar, 1998) and the relatively low energetic cost of the transfer of absorbed FA to milk fat when compared with the cost of de novo synthesis of FA (Bauman et al., 1985).

Furthermore, it is important to note that from a practical feeding perspective, the increase in maintenance requirements in modern milk production systems may be partially balanced by the simultaneous increase in the efficiency of dietary ME utilization. For example, assuming no tissue gain or loss and a BW of 600 kg, the ME_M and k_L values of the structural equation model result in total ME expenditure to be in balance in these 3 decades at an ECM production of about 38 kg/d. Compared with the third decade, animals in the first decade are more efficient at ECM production levels below 38 kg/d and less efficient at ECM production levels above 38 kg/d. Finally, it is also important to note that maintenance requirements and efficiency estimates are inherently correlated within a model, as pointed out by Moe (1981), who described lower efficiencies as a consequence of lower maintenance costs. Therefore, estimated energetic parameters for a given model and decade should be simultaneously used in the prediction of energy utilization by lactating cows.

CONCLUSIONS

A multivariate framework was proposed to analyze energy balance data from lactating cows which accounted for the variation in ME intake, milk energy output, and tissue energy balance and allowed for these traits to have simultaneous and recursive relationships. The proposed model was compared with methods traditionally used to estimate maintenance requirements and energetic efficiencies. Maintenance requirements and partial efficiencies of utilizing dietary energy and body stores, estimated in both models, were similar to values proposed in the literature. In particular, for the proposed model, NE_M was 0.36 MJ/kg of $BW^{0.75}$·day, and k_L, k_G, and k_T were 0.63, 0.70, and 0.89, respectively. Additional analyses were conducted in which energetic parameters were allowed to depend on the decade of the study to investigate potential changes in maintenance requirements and partial efficiencies across decades. For both models, NE_M, k_L, and k_G increased for the more recent decades whereas k_T remained unchanged. The increase in maintenance requirements in contemporary milk production systems is consistent with the literature that describes increased fasting heat production in cows of higher genetic merit. The increase in the efficiency of utilizing dietary energy was partially attributed to the changes in dietary composition, in particular to the increase in dietary ether extract to levels closer to those currently observed in milk production systems. Finally, the estimated energetic parameters from this study can be used to update maintenance requirements and partial efficiencies of energy utilization in North American feeding systems.

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APPENDIX 1

Bayesian implementation of the energy balance models and description of the canonical correlation analysis.

Bayesian Implementation of the Univariate Model

The conditional density of the data given the location parameters $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, and $\boldsymbol{\delta}$, and the variance, σ^2, was assumed to be:

$$\mathbf{y}|\boldsymbol{\beta},\ \boldsymbol{\alpha},\ \boldsymbol{\delta},\ \sigma^2 \sim N(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta},\ \sigma^2\mathbf{I_n}),$$

where $\mathbf{y}$ is the $n \times 1$ vector of milk energy outputs; $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are known design matrices relating elements of $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, and $\boldsymbol{\delta}$, to $\mathbf{y}$; $\boldsymbol{\beta}$ is the $m \times 1$ vector of regression coefficients; $\boldsymbol{\alpha}$ is the vector of $mn_a \times 1$ animal random regression coefficients; and $\boldsymbol{\delta}$ is the vector of $mn_s \times 1$ study random regression coefficients. In this notation, n represents the number of observations; n_s and n_a are the number of studies and animals, respectively.

The following joint prior distribution, given a set of known hyperparameters, was assumed:

$$p(\boldsymbol{\beta},\ \boldsymbol{\alpha},\ \boldsymbol{\delta},\ \sigma^2,\ \mathbf{G}_{\boldsymbol{\alpha}},\ \mathbf{G}_{\boldsymbol{\delta}}|H) = N(\boldsymbol{\beta}|\mathbf{1}b_0,\mathbf{I_m}\tau^2)N(\boldsymbol{\alpha}|\mathbf{0},\mathbf{G}_{\boldsymbol{\alpha}})$$
$$\times\ N(\boldsymbol{\delta}|\mathbf{0},\mathbf{G}_{\boldsymbol{\delta}})\mathrm{IG}(\sigma^2|a,b)\mathrm{IW}(\mathbf{G}_{\boldsymbol{\alpha}}|\mathbf{V}_{\boldsymbol{\alpha}},v_\alpha)\mathrm{IW}(\mathbf{G}_{\boldsymbol{\delta}}|\mathbf{V}_{\boldsymbol{\delta}},v_\delta),$$

where $H = \{b_0,\tau^2,a,b,\ \mathbf{V}_{\boldsymbol{\alpha}},v_\alpha,\ \mathbf{V}_{\boldsymbol{\delta}},v_\delta\}$ is the set of known hyperparameters; $N(\boldsymbol{\beta}|\mathbf{1}b_0,\mathbf{I_m}\tau^2)$ is a multivariate normal density; $\mathbf{1}$ is a $m \times 1$ vector of ones; b_0 is the prior mean common to all β; $\mathbf{I_m}$ is the identity matrix of order m; τ^2 is the variance parameter specifying the degree of sharpness of the prior density; $N(\boldsymbol{\alpha}|\mathbf{0},\mathbf{G}_{\boldsymbol{\alpha}})$ and $N(\boldsymbol{\delta}|\mathbf{0},\mathbf{G}_{\boldsymbol{\delta}})$ are multivariate normal densities centered at zero with covariance matrices $\mathbf{G}_{\boldsymbol{\alpha}}$ and $\mathbf{G}_{\boldsymbol{\delta}}$; and $\mathrm{IG}(\sigma^2|a,b)$ is the inverse gamma density with scale parameter a and shape parameter b. Further, $\mathrm{IW}(\mathbf{G}_{\boldsymbol{\alpha}}|\mathbf{V}_{\boldsymbol{\alpha}},v_\alpha)$ and $\mathrm{IW}(\mathbf{G}_{\boldsymbol{\delta}}|\mathbf{V}_{\boldsymbol{\delta}},v_\delta)$ are inverse Wishart densities with scale matrices $\mathbf{V}_{\boldsymbol{\alpha}}$ and $\mathbf{V}_{\boldsymbol{\delta}}$, and degrees of freedom v_α and v_δ. The Bayes theorem gives that the posterior distribution is proportional to the product of the density of the data and the joint prior density. Therefore, the joint posterior distribution is given by

$$p(\boldsymbol{\beta},\boldsymbol{\alpha},\boldsymbol{\delta},\sigma^2,\mathbf{G}_{\boldsymbol{\alpha}},\mathbf{G}_{\boldsymbol{\delta}}|\mathbf{y},H) \propto N(\mathbf{y}|\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta},\sigma^2\mathbf{I_n})$$
$$\times\ N(\boldsymbol{\beta}|\mathbf{1}b_0,\mathbf{I_m}\tau^2)N(\boldsymbol{\alpha}|\mathbf{0},\mathbf{G}_{\boldsymbol{\alpha}})N(\boldsymbol{\delta}|\mathbf{0},\mathbf{G}_{\boldsymbol{\delta}})\mathrm{IG}(\sigma^2|a,b)$$
$$\times\ \mathrm{IW}(\mathbf{G}_{\boldsymbol{\alpha}}|\mathbf{V}_{\boldsymbol{\alpha}},v_\alpha)\mathrm{IW}(\mathbf{G}_{\boldsymbol{\delta}}|\mathbf{V}_{\boldsymbol{\delta}},v_\delta).$$

Minimally informative distributions were specified for the priors so they have minor influence in the posterior distributions and the inference is mostly influenced by the observed data (Gelman et al., 2004). Specifically, we set $b_0 = 0$ and $\tau^2 = 10^6$. Hyperparameters of the inverse gamma density were set such that $\mathrm{E}(\sigma^2|a,b) = 1$ and $\mathrm{Var}(\sigma^2|a,b) = 10^3$. Similarly, hyperparameters of the inverse Wishart densities were specified with the degrees of freedom equal to m and the scale matrix as $diag\{10^3,\ldots,10^3\}$, as suggested by Lunn et al. (2000) in the construction of minimally informative prior densities for covariance matrices.

Bayesian Implementation of the Multivariate Model

The Bayesian implementation of the model followed results from Gianola and Sorensen (2004). In particular, given the location parameters $\boldsymbol{\Lambda}_\mathbf{0}$, $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, $\boldsymbol{\delta}$, and the covariance matrix, $\mathbf{R}$, the density of the vector $\boldsymbol{\Lambda}\mathbf{y}$ was assumed to be

$$\boldsymbol{\Lambda}\mathbf{y}|\boldsymbol{\Lambda}_\mathbf{0},\ \boldsymbol{\beta},\ \boldsymbol{\alpha},\ \boldsymbol{\delta},\ \mathbf{R} \sim N(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta},\mathbf{I_n} \otimes \mathbf{R}),$$

where $\mathbf{y}$ is the $3n \times 1$ vector composed of ME intakes, milk energy outputs and tissue energy balances; $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are known design matrices relating elements of $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, and $\boldsymbol{\delta}$ to $\mathbf{y}$; $\boldsymbol{\beta}$ is the $m \times 1$ vector of regression coefficients ($m = \sum_{r=1}^{3} m_r$, where m_r is the number of regression parameters for the rth response, where the responses are ME intake, milk energy output, and tissue energy balance); $\boldsymbol{\alpha}$ is the $mn_a \times 1$ vector of animal

random regression coefficients; and $\boldsymbol{\delta}$ is the $mn_s \times 1$ vector of study random regression coefficients. In this notation, n represents the number of observations, n_a the number of animals and n_s the number of studies. Further, $\boldsymbol{\Lambda} = \mathbf{I_n} \otimes \boldsymbol{\Lambda_0}$, where the unknown elements of $\boldsymbol{\Lambda_0}$ are collected in $\boldsymbol{\lambda}$, which is modeled as $\boldsymbol{\lambda} = \mathbf{W}\boldsymbol{\lambda_\mu} + \mathbf{Z}_3\boldsymbol{\zeta} + \mathbf{Z}_4\boldsymbol{\xi}$, where $\mathbf{W}$, $\mathbf{Z}_3$, and $\mathbf{Z}_4$ are known incidence matrices relating elements of $\boldsymbol{\lambda_\mu}$, $\boldsymbol{\varsigma}$, and $\boldsymbol{\xi}$ to elements in $\boldsymbol{\lambda}$; $\boldsymbol{\lambda_\mu}$ is the $k \times 1$ vector of population structural coefficients; $\boldsymbol{\zeta}$ and $\boldsymbol{\xi}$ are $kn_a \times 1$ and $kn_s \times 1$ vectors of animal and study random coefficients respectively. Moreover, $\mathbf{R}$ is an unstructured covariance matrix of order 3, $\mathbf{G_\alpha}$ and $\mathbf{G_\delta}$ are unstructured covariance matrices of order m, and $\mathbf{G_\zeta}$ and $\mathbf{G_\xi}$ are unstructured covariance matrices of order k. Moreover, Gianola and Sorensen (2004) used the result that the determinant of the Jacobian in the variable transformation from $\boldsymbol{\Lambda}\mathbf{y}$ to $\mathbf{y}$ is $|\boldsymbol{\Lambda}|$ and, with $\boldsymbol{\Lambda}$ of full rank, to derive the conditional density of $\mathbf{y}$:

$$\mathbf{y}|\boldsymbol{\Lambda_0},\boldsymbol{\beta},\boldsymbol{\alpha},\boldsymbol{\delta},\mathbf{R} \sim N[\boldsymbol{\Lambda}^{-1}(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta}), \boldsymbol{\Lambda}^{-1}(\mathbf{I_n} \otimes \mathbf{R})(\boldsymbol{\Lambda}^{-1})^{\mathrm{T}}].$$

The joint prior distribution of all unknowns, given a set of known hyperparameters, was assumed to be:

$$p(\boldsymbol{\beta},\boldsymbol{\lambda_\mu},\boldsymbol{\alpha},\boldsymbol{\delta},\mathbf{R},\mathbf{G_\zeta},\mathbf{G_\xi},\mathbf{G_\alpha},\mathbf{G_\delta} \mid H) = N(\boldsymbol{\beta} \mid \mathbf{1}b_0, \mathbf{I_m}\tau_0^2) \times N(\boldsymbol{\lambda_\mu} \mid \mathbf{1}b_1, \mathbf{I_k}\tau_1^2) N(\boldsymbol{\zeta} \mid \mathbf{0}, \mathbf{G_\zeta}) N(\boldsymbol{\xi} \mid \mathbf{0}, \mathbf{G_\xi}) N(\boldsymbol{\alpha} \mid \mathbf{0}, \mathbf{G_\alpha}) \times N(\boldsymbol{\delta} \mid \mathbf{0}, \mathbf{G_\delta}) \mathrm{IW}(\mathbf{R} \mid \mathbf{V_R}, \nu_\mathrm{R}) \mathrm{IW}(\mathbf{G_\zeta} \mid \mathbf{V_\zeta}, \nu_\zeta) \mathrm{IW}(\mathbf{G_\xi} \mid \mathbf{V_\xi}, \nu_\xi) \times \mathrm{IW}(\mathbf{G_\alpha} \mid \mathbf{V_\alpha}, \nu_\alpha) \mathrm{IW}(\mathbf{G_\delta} \mid \mathbf{V_\delta}, \nu_\delta),$$

where

$$H = \left\{b_0, \tau_0^2, b_1, \tau_1^2, \mathbf{V_R}, \nu_\mathrm{R}, \mathbf{V_\zeta}, \nu_\zeta, \mathbf{V_\xi}, \nu_\xi, \mathbf{V_\alpha}, \nu_\alpha, \mathbf{V_\delta}, \nu_\delta\right\}$$

is the set of known hyperparameters, $N(\boldsymbol{\beta} \mid \mathbf{1}b_0, \mathbf{I_m}\tau_0^2)$ and $N(\boldsymbol{\lambda_\mu} \mid \mathbf{1}b_1, \mathbf{I_k}\tau_1^2)$ are multivariate normal densities with prior means b_0 and b_1, and variance parameters τ_0^2 and τ_1^2, respectively. Further, $N(\boldsymbol{\zeta}|\mathbf{0},\mathbf{G_\zeta})$, $N(\boldsymbol{\xi}|\mathbf{0},\mathbf{G_\xi})$, $N(\boldsymbol{\alpha}|\mathbf{0},\mathbf{G_\alpha})$, and $N(\boldsymbol{\delta}|\mathbf{0},\mathbf{G_\delta})$ are multivariate normal densities centered at zero and with covariance matrices $\mathbf{G_\zeta}$, $\mathbf{G_\xi}$, $\mathbf{G_\alpha}$, and $\mathbf{G_\delta}$. Similarly, $\mathrm{IW}(\mathbf{R}|\mathbf{V_R},\upsilon_\mathrm{R})$, $\mathrm{IW}(\mathbf{G_\zeta}|\mathbf{V_\zeta},\upsilon_\zeta)$, $\mathrm{IW}(\mathbf{G_\xi}|\mathbf{V_\xi},\upsilon_\xi)$, $\mathrm{IW}(\mathbf{G_\alpha}|\mathbf{V_\alpha},\upsilon_\alpha)$, and $\mathrm{IW}(\mathbf{G_\delta}|\mathbf{V_\delta},\upsilon_\delta)$ are inverse Wishart densities with scale matrices $\mathbf{V_R}$, $\mathbf{V_\zeta}$, $\mathbf{V_\xi}$, $\mathbf{V_\alpha}$, and $\mathbf{V_\delta}$, and degrees of freedom υ_R, υ_ζ, υ_ξ, υ_α, and υ_δ. The joint posterior distribution is then proportional to the conditional density of the data times the joint prior density:

$$p(\boldsymbol{\beta},\boldsymbol{\lambda_\mu},\boldsymbol{\alpha},\boldsymbol{\delta},\mathbf{R},\mathbf{G_\zeta},\mathbf{G_\xi},\mathbf{G_\alpha},\mathbf{G_\delta} \mid \mathbf{y}, H) \propto N\left[\mathbf{y} \mid \boldsymbol{\Lambda}^{-1}\left(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{\alpha} + \mathbf{Z}_2\boldsymbol{\delta}\right),\ \boldsymbol{\Lambda}^{-1}(\mathbf{I_n} \otimes \mathbf{R})(\boldsymbol{\Lambda}^{-1})^{\mathrm{T}}\right] \times N(\boldsymbol{\beta} \mid \mathbf{1}b_0, \mathbf{I_m}\tau_0^2) N(\boldsymbol{\lambda_\mu} \mid \mathbf{1}b_1, \mathbf{I_k}\tau_1^2) N(\boldsymbol{\zeta} \mid \mathbf{0}, \mathbf{G_\zeta}) N(\boldsymbol{\xi} \mid \mathbf{0}, \mathbf{G_\xi}) \times N(\boldsymbol{\alpha} \mid \mathbf{0}, \mathbf{G_\alpha}) N(\boldsymbol{\delta} \mid \mathbf{0}, \mathbf{G_\delta}) \mathrm{IW}(\mathbf{R} \mid \mathbf{V_R}, \nu_\mathrm{R}) \mathrm{IW}(\mathbf{G_\zeta} \mid \mathbf{V_\zeta}, \nu_\zeta) \times \mathrm{IW}(\mathbf{G_\xi} \mid \mathbf{V_\xi}, \nu_\xi) \mathrm{IW}(\mathbf{G_\alpha} \mid \mathbf{V_\alpha}, \nu_\alpha) \mathrm{IW}(\mathbf{G_\delta} \mid \mathbf{V_\delta}, \nu_\delta).$$

Minimally informative distributions were specified for the priors so they have minor influence in the posterior distributions and the inference is mostly influenced by the data (Gelman et al., 2004), as described in the previous section.

Canonical Correlation Analysis

Let $\boldsymbol{\theta}$ be an $m \times 1$ vector of estimated mixed effects representing the energetic parameters and $\boldsymbol{\eta}$ be the $t \times 1$ vector of variables describing dietary and animal characteristics. It is assumed that $\mathrm{Var}\begin{bmatrix}\boldsymbol{\theta}\\ \boldsymbol{\eta}\end{bmatrix} = \begin{bmatrix}\mathbf{V}_{11} & \mathbf{V}_{12}\\ \mathbf{V}_{21} & \mathbf{V}_{22}\end{bmatrix}$, where $\mathrm{Var}(\boldsymbol{\theta}) = \mathbf{V}_{11}$, $\mathrm{Var}(\boldsymbol{\eta}) = \mathbf{V}_{22}$, and $\mathbf{V}_{12} = \mathrm{Cov}\left(\boldsymbol{\theta},\ \boldsymbol{\eta}\right) = \mathbf{V}_{21}^{\mathrm{T}}$ for $\mathbf{V}_{11}$ and $\mathbf{V}_{22}$ of full rank. Canonical correlation analysis identifies vectors $\mathbf{a}$ and $\mathbf{b}$ $\left(\mathbf{a} \in \mathbb{R}^m \text{ and } \mathbf{b} \in \mathbb{R}^t\right)$ such that the correlation between the linear combinations $\mathbf{a}^{\mathrm{T}}\boldsymbol{\theta}$ and $\mathbf{b}^{\mathrm{T}}\boldsymbol{\eta}$ are maximized. In particular, the function $\rho = \max_{\mathbf{a},\mathbf{b}}\left\{\frac{\mathbf{a}^{\mathrm{T}}\mathbf{V}_{12}\mathbf{b}}{\sqrt{\mathbf{a}^{\mathrm{T}}\mathbf{V}_{11}\mathbf{a}\mathbf{b}^{\mathrm{T}}\mathbf{V}_{22}\mathbf{b}}}\right\}$ may be maximized with generalized eigenvalues. Specifically, let $\lambda_1 \geq \ldots \geq \lambda_h$ be the eigenvalues of $\mathbf{V}_{11}^{-1/2}\mathbf{V}_{12}\mathbf{V}_{22}^{-1}\mathbf{V}_{21}\mathbf{V}_{11}^{-1/2}$ with $\mathbf{u}_1,\ldots,\mathbf{u}_h$ as the corresponding orthonormal eigenvectors. The maximum and the arguments of the maximum are given by $\rho_\mathrm{i} = \lambda_i^{1/2}$, $\mathbf{a}_i = \mathbf{V}_{11}^{-1/2}\mathbf{u}_i$, $\mathbf{b}_i = \lambda_i^{-1/2}\mathbf{V}_{22}\mathbf{V}_{21}\mathbf{V}_{11}^{-1/2}\mathbf{u}_i$, and $i = 1,\ldots,h = \min(m,\ t)$, where $\rho_1 \geq \ldots \geq \rho_h$ are the canonical correlations, $\mathbf{a}_1^{\mathrm{T}}\boldsymbol{\theta}$, ... , $\mathbf{a}_h^{\mathrm{T}}\boldsymbol{\theta}$ are the canonical variates of $\boldsymbol{\theta}$ and $\mathbf{b}_1^{\mathrm{T}}\boldsymbol{\eta}$, ... , $\mathbf{b}_h^{\mathrm{T}}\boldsymbol{\eta}$ are the canonical variates of $\boldsymbol{\eta}$. Notice that $\mathbf{V}_{11}^{-1/2}$ can be calculated by the eigen-decomposition $\mathbf{V}_{11} = \mathbf{Q}\mathbf{D}\mathbf{Q}^{\mathrm{T}}$. For instance, $\mathbf{V}_{11}^{-1/2} = \mathbf{Q}\mathbf{D}^{-1/2}\mathbf{Q}^{\mathrm{T}}$, where $\mathbf{Q}$ is the matrix for which columns are eigenvectors $\mathbf{q}_1,\ldots,\mathbf{q}_m$ corresponding to the eigenvalues $\lambda_{(q),1},\ldots,\lambda_{(q)}{}_m$ of $\mathbf{V}_{11}$ and $\mathbf{D}^{-1/2} = diag\{\lambda_{(q),1}^{-1/2}, ..., \lambda_{(q),m}^{-1/2}\}$.

APPENDIX 2

Posterior means and 95% credible intervals (in parentheses) of model parameters and variance components for the Strathe et al. (2011) and structural equation (**SEqM**) models with study decade-specific parameters.

Table A2.1. Parameters posterior means and 95% credible intervals (in parentheses) using the Strathe et al. (2011) and the SEqM models[1]

Parameter	Strathe et al. (2011)	SEqM
β_0	–0.35 (–0.38, –0.32)	—
β_1	0.62 (0.60, 0.64)	0.57 (0.56, 0.58)
β_2	0.83 (0.79, 0.87)	–0.36 (–0.38, –0.34)
β_3	0.80 (0.76, 0.84)	–0.40 (–0.42, –0.37)
λ_{21}	—	0.63 (0.61, 0.64)
$\lambda_{23}^{(1)}$	—	–0.90 (–0.92, –0.88)
$\lambda_{23}^{(2)}$	—	–0.89 (–0.91, –0.87)
λ_{31}	—	0.70 (0.68, 0.72)
λ_{32}	—	–1.11 (–1.13, –1.09)

[1]β = regression coefficients; λ = structural parameters of the structural equation model. Note that β in the 2 different models represent different parameters that are not directly comparable.

Table A2.2. Parameters posterior means and 95% credible intervals (in parentheses) for the Strathe et al. (2011) and the SEqM for the 3 decades for which studies were conducted

Parameter[1]	Decade	Strathe et al. (2011)	SEqM
β_0	1963–1973	–0.30 (–0.33, –0.27)	—
β_0	1974–1983	–0.36 (–0.41, –0.32)	—
β_0	1984–1995	–0.48 (–0.53, –0.42)	—
β_1	1963–1973	0.60 (0.58, 0.62)	0.56 (0.55, 0.58)
β_1	1974–1983	0.62 (0.59, 0.65)	0.57 (0.55, 0.59)
β_1	1984–1995	0.68 (0.65, 0.71)	0.57 (0.55, 0.59)
β_2	1963–1973	0.88 (0.83, 0.94)	–0.31 (–0.33, –0.28)
β_2	1974–1983	0.79 (0.72, 0.86)	–0.37 (–0.41, –0.34)
β_2	1984–1995	0.80 (0.74, 0.86)	–0.52 (–0.56, –0.47)
β_3	1963–1973	0.82 (0.76, 0.87)	–0.34 (–0.36, –0.31)
β_3	1974–1983	0.81 (0.73, 0.87)	–0.41 (–0.45, –0.37)
β_3	1984–1995	0.79 (0.70, 0.86)	–0.57 (–0.62, –0.52)
λ_{21}	1963–1973	—	0.60 (0.58, 0.62)
λ_{21}	1974–1983	—	0.63 (0.60, 0.65)
λ_{21}	1984–1995	—	0.70 (0.68, 0.73)
$\lambda_{23}^{(1)}$	1963–1973	—	–0.90 (–0.92, –0.89)
$\lambda_{23}^{(1)}$	1974–1983	—	–0.90 (–0.93, –0.88)
$\lambda_{23}^{(1)}$	1984–1995	—	–0.90 (–0.92, –0.88)
$\lambda_{23}^{(2)}$	1963–1973	—	–0.91 (–0.92, –0.88)
$\lambda_{23}^{(2)}$	1974–1983	—	–0.90 (–0.92, –0.88)
$\lambda_{23}^{(2)}$	1984–1995	—	–0.90 (–0.92, –0.88)
λ_{31}	1963–1973	—	0.66 (0.64, 0.69)
λ_{31}	1974–1983	—	0.70 (0.67, 0.72)
λ_{31}	1984–1995	—	0.78 (0.75, 0.81)
λ_{32}	1963–1973	—	–1.10 (–1.12, –1.08)
λ_{32}	1974–1983	—	–1.11(–1.13, –1.08)
λ_{32}	1984–1995	—	–1.10 (–1.13, –1.08)

[1]β = regression coefficients; λ = structural parameters of the structural equation model. Note that β in the 2 different models represent different parameters that are not directly comparable.

Table A2.3. Variance components posterior means and 95% credible intervals (in parentheses) for the Strathe et al. (2011) model

Parameter[1]	Estimate
σ^2	0.00112 (0.00100, 0.00126)
$G_{\alpha}^{(11)}$	0.00111 (0.00022, 0.00301)
$G_{\alpha}^{(22)}$	0.00044 (0.00012, 0.00117)
$G_{\alpha}^{(33)}$	0.00148 (0.00015, 0.00694)
$G_{\alpha}^{(44)}$	0.00071 (0.00013, 0.00250)
$G_{\alpha}^{(12)}$	–0.00044 (–0.00157, 0.00005)
$G_{\alpha}^{(13)}$	0.00031 (–0.00118, 0.00247)
$G_{\alpha}^{(14)}$	0.00012 (–0.00092, 0.00148)
$G_{\alpha}^{(23)}$	–0.00030 (–0.00179, 0.00046)
$G_{\alpha}^{(24)}$	–0.00004 (–0.00078, 0.00058)
$G_{\alpha}^{(34)}$	–0.00007 (–0.00169, 0.00126)
$G_{\delta}^{(11)}$	0.00108 (0.00019, 0.00336)
$G_{\delta}^{(22)}$	0.00038 (0.00010, 0.00109)
$G_{\delta}^{(33)}$	0.00120 (0.00017, 0.00437)
$G_{\delta}^{(44)}$	0.00257 (0.00031, 0.00803)
$G_{\delta}^{(12)}$	–0.00043 (–0.00164, 0.00002)
$G_{\delta}^{(13)}$	–0.00045 (–0.00247, 0.00060)
$G_{\delta}^{(14)}$	0.00078 (–0.00068, 0.00359)
$G_{\delta}^{(23)}$	0.00018 (–0.00043, 0.00124)
$G_{\delta}^{(24)}$	–0.00041 (–0.00191, 0.00039)
$G_{\delta}^{(34)}$	–0.00010 (–0.00330, 0.00187)

[1]σ^2 = residual variance; G_{α} = variance components associated with the animal random regression coefficients; G_{δ} = variance components associated with the study random regression coefficients.

Table A2.4. Variance components posterior means and 95% credible intervals (in parentheses) for the structural equation model

Parameter[1]	Estimate
$R^{(11)}$	0.006629 (0.006010, 0.007305)
$R^{(22)}$	0.001305 (0.001169, 0.001452)
$R^{(33)}$	0.001600 (0.001440, 0.001769)
$R^{(12)}$	0.000833 (0.000610, 0.001068)
$R^{(13)}$	0.000923 (0.000681, 0.001179)
$R^{(23)}$	0.001443 (0.001299, 0.001597)
$G_{\alpha}^{(11)}$	0.000134 (0.000077, 0.000206)
$G_{\alpha}^{(22)}$	0.000489 (0.000144, 0.000829)
$G_{\alpha}^{(33)}$	0.000598 (0.000172, 0.001015)
$G_{\alpha}^{(12)}$	0.000015 (–0.000070, 0.000108)
$G_{\alpha}^{(13)}$	0.000016 (–0.000077, 0.000119)
$G_{\alpha}^{(23)}$	0.000531 (0.000149, 0.000909)
$G_{\delta}^{(11)}$	0.000923 (0.000540, 0.001540)
$G_{\delta}^{(22)}$	0.000306 (0.000107, 0.000633)
$G_{\delta}^{(33)}$	0.000365 (0.000123, 0.000759)
$G_{\delta}^{(12)}$	–0.000119 (–0.000389, 0.000118)
$G_{\delta}^{(13)}$	–0.000130 (–0.000427, 0.000139)
$G_{\delta}^{(23)}$	0.000295 (0.000080, 0.000647)
$G_{\zeta}^{(11)}$	0.000144 (0.000049, 0.000288)
$G_{\zeta}^{(22)}$	0.000050 (0.000031, 0.000078)
$G_{\zeta}^{(33)}$	0.000047 (0.000029, 0.000075)
$G_{\zeta}^{(44)}$	0.000175 (0.000059, 0.000357)
$G_{\zeta}^{(55)}$	0.000045 (0.000028, 0.000071)
$G_{\zeta}^{(12)}$	–0.000004 (–0.000043, 0.000033)
$G_{\zeta}^{(13)}$	–0.000002 (–0.000037, 0.000034)
$G_{\zeta}^{(14)}$	0.000150 (0.000046, 0.000310)
$G_{\zeta}^{(15)}$	0.000007 (–0.000031, 0.000044)
$G_{\zeta}^{(23)}$	0.000002 (–0.000014, 0.000019)
$G_{\zeta}^{(24)}$	0.000005 (–0.000037, 0.000048)
$G_{\zeta}^{(25)}$	–0.000017 (–0.000038, −0.000002)
$G_{\zeta}^{(34)}$	0.000003 (–0.000034, 0.000044)
$G_{\zeta}^{(35)}$	–0.000016 (–0.000037, –0.000002)
$G_{\zeta}^{(45)}$	–0.000009 (–0.000053, 0.000030)
$G_{\xi}^{(11)}$	0.000119 (0.000051, 0.000245)
$G_{\xi}^{(22)}$	0.000078 (0.000041, 0.000143)
$G_{\xi}^{(33)}$	0.000078 (0.000041, 0.000140)
$G_{¾}^{(44)}$	0.000145 (0.000059, 0.000310)
$G_{\xi}^{(55)}$	0.000077 (0.000041, 0.000144)
$G_{\xi}^{(12)}$	–0.000004 (–0.000056, 0.000045)
$G_{\xi}^{(13)}$	–0.000003 (–0.000053, 0.000046)
$G_{\xi}^{(14)}$	0.000093 (0.000022, 0.000228)
$G_{\xi}^{(15)}$	0.000005 (–0.000044, 0.000057)
$G_{\xi}^{(23)}$	0.000007 (–0.000027, 0.000048)
$G_{\xi}^{(24)}$	0.000012 (–0.000041, 0.000074)
$G_{\xi}^{(25)}$	–0.000025 (–0.000074, 0.000007)
$G_{\xi}^{(34)}$	0.000010 (–0.000043, 0.000070)
$G_{\xi}^{(35)}$	–0.000022 (–0.000069, 0.000010)
$G_{\xi}^{(45)}$	–0.000017 (–0.000083, 0.000034)

[1]R = residual variance components; G_{α} = variance components associated with the animal random regression coefficients; G_{δ} = variance components associated with the study random regression coefficients; G_{ζ} = variance components associated with the structural animal random coefficients; G_{ξ} = variance components associated with the structural study random coefficients.

APPENDIX 3

Diagnostic plots of the Strathe et al. (2011) and structural equation models.

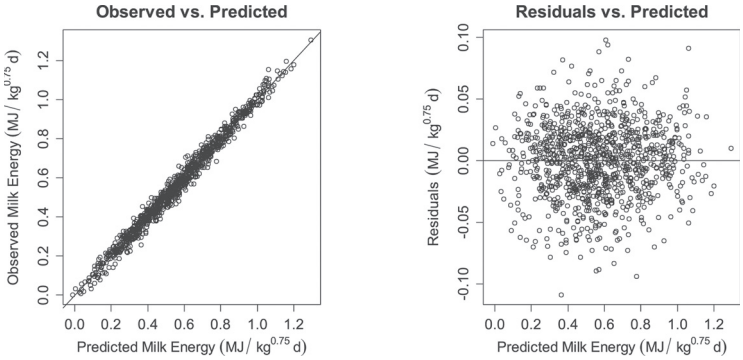

Figure A3.1. Diagnostics of the model from Strathe et al. (2011).

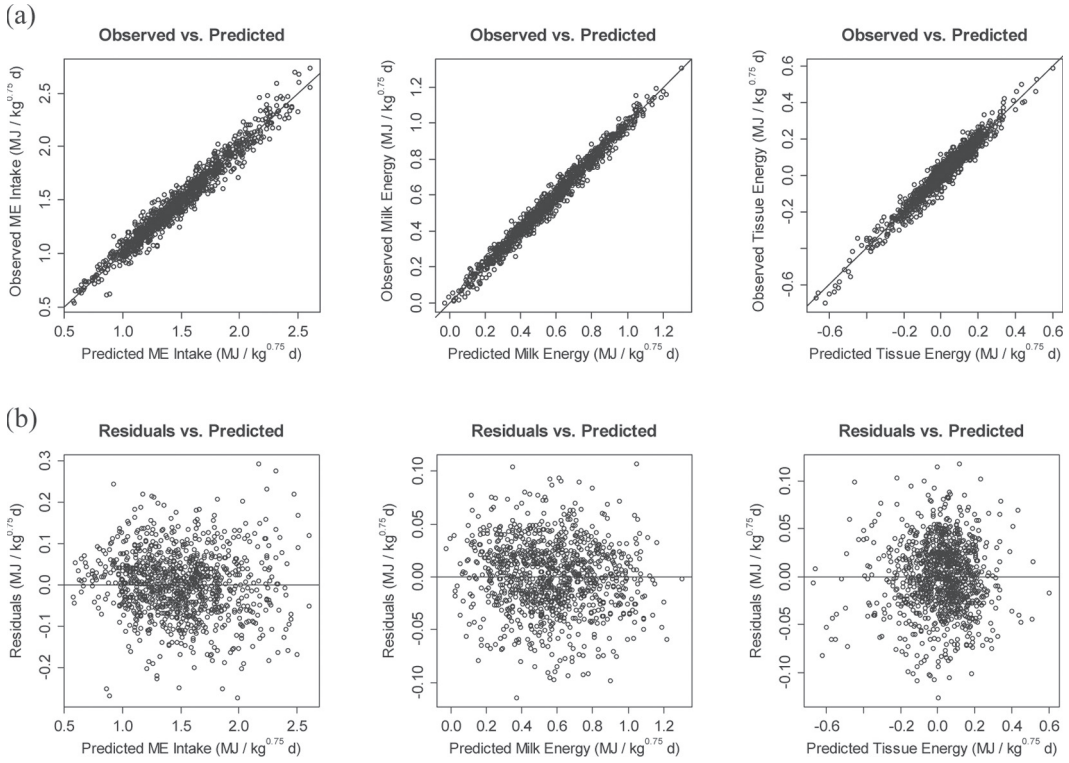

Figure A3.2. Diagnostics of the structural equation model for (a) observed versus predicted values and (b) residuals versus predicted values.